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Enhancement of drought stress tolerance in crops by plant growth promoting rhizobacteria

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ABSTRACT

Drought is one of the major constraints on agricultural productivity worldwide and is likely to further increase. Several adaptations and mitigation strategies are required to cope with drought stress. Plant growth promoting rhizobacteria (PGPR) could play a significant role in alleviation of drought stress in plants. These beneficial microorganisms colonize the rhizosphere/endo-rhizosphere of plants and impart drought tolerance by producing exopolysaccharides (EPS), phytohormones, 1-aminocyclopropane- 1-carboxylate (ACC) deaminase, volatile compounds, inducing accumulation of osmolytes, antioxidants, upregulation or down regulation of stress responsive genes and alteration in root morphology in acquisition of drought tolerance. The term Induced Systemic Tolerance (IST) was coined for physical and chemical changes induced by microorganisms in plants which results in enhanced tolerance to drought stresses. In the present review we elaborate on the role of PGPR in helping plants to cope with drought stress.
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Abbreviations: PGPR, plant growth promoting rhizobacteria; PGPB, plant growth promoting bacteria; EPS, exopolysaccharides; ACC, 1-aminocyclopropane- 1-carboxylate; IST, induced systemic tolerance; ROS, reactive oxygen species; NR, nitrate reductase; ABA, abscisic acid; IAA, indole -3-acetic acid; ACS, 1-aminocyclopropane-1-carboxylate synthase; S-AdoMet, S-adenosylmethionine; PSB, phosphate solubilising bacteria; GB, glycine betine; RWC, relative water content; DMW, dry mater weight; LP, lipopolysaccharide–protein; PL, polysaccharide–lipid; RAS/RT, root adhering soil per root tissue; $O_2^{\bullet -}$, superoxide anion radicals; H_2O_2, hydrogen peroxide; OH, hydroxyl radicals; $^1O_2$, singlet oxygen; RO, alkoxy radicals; SOD, superoxide dismutase; CAT, catalase; APX, ascorbate peroxidase; GR, glutathione reductase; GPX, glutathione peroxidase; MDA, malondialdehyde; ERD15, early response to dehydration 15; 2D-PAGE, 2-D polyacrylamide gel electrophoresis; DD-PCR, differential display polymerase chain reaction; RT-PCR, real-time PCR; AM, arbuscular mycorrhizal; Rubisco, ribulose-1,5-bisphosphate carboxy/oxygenase; PGP, plant growth promoting.

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1. Introduction

Drought stress is among the most destructive abiotic stresses that increased in intensity over the past decades affecting world's food security. Drought stress may range from moderate and short to extremely severe and prolonged duration, restricting the crop yields (Austin, 1989; Pereira and Chaves, 1993, 1995; Bottner et al., 1995). Drought is expected to cause serious plant growth problems for more than 50% of the arable lands by 2050 (Ashraf, 1994; Vinocur and Altman, 2005; Kasim et al., 2013).

1.1. Effect of drought stress on plant growth and development

Drought affects plant–water potential and turgor, enough to interfere with normal functions (Hsiao 2000) changing physiological and morphological traits in plants (Rahdari and Hoseini, 2012). Growth reduction under drought stress has been studied in several crops such as barley (Samarah, 2005), maize (Kamara et al., 2003), rice (Lafitte et al., 2007) and wheat (Rampino et al., 2006). Fresh weight and water content are common growth parameters that are affected by drought (Jaleel et al., 2009). Furthermore, drought stress influences the availability and transport of soil nutrients, as nutrients are carried to the roots by water. Drought stress therefore decreases nutrient diffusion and mass flow of water-soluble nutrients such as nitrate, sulfate, Ca, Mg, and Si (Barber, 1995; Selvakumar et al., 2012). Drought also induces free radicals affecting antioxidant defenses and Reactive Oxygen Species (ROS) such as superoxide radicals, hydrogen peroxide and hydroxyl radicals resulting in oxidative stress. At high concentrations ROS can cause damage to various levels of organization (Smirnoff, 1993), like initiate lipid peroxidation, membrane deterioration and degrade proteins, lipids and nucleic acids in plants (Hendry, 2005; Sgherri et al., 2000; Nair et al., 2008). Nevertheless, under drought stress the decrease in chlorophyll content was symptom of photooxidation (Anjum et al., 2011; Rahdari et al., 2012). Decreasing of chlorophyll content in *Paulownia imperialis* (Astorga and Melendez, 2010), bean (Beinsan et al., 2003) and *Carthamus tinctorius* (Siddiqi et al., 2009) was observed under drought stress. Drought also affects biochemical activities like nitrate reductase (NR), due to lower uptake of nitrate from the soil (Caravaca et al., 2005). It also accentuates the biosynthesis of ethylene, which inhibits plant growth through several mechanisms (Ali et al., 2014). Drought as a multidimensional stress, affects at various sub cellular compartment, cell organs and whole plant level (Choluj et al., 2004; Rahdari et al., 2012). Thus drought negatively affects quantity and quality of growth in plants. Therefore, in order to produce more food, the mitigation of drought stresses is important to achieve the designated goals.

Worldwide extensive research is being carried out to develop strategies to cope with drought stress through development of drought tolerant varieties, shifting the crop calendars, resource management practices etc. (Venkateswarlu and Shanker, 2009) and most of these technologies are cost-intensive. Recent studies indicate that microorganisms can also help plants to cope with drought stress.

1.2. Drought stress microbial ecology

Millions of microbes inhabit plant root system forming a complex ecological community that influences plant growth and productivity through its metabolic activities and plant interactions (Berg, 2009; Lugtenberg and Kamilova, 2009; Schmidt et al., 2014). Changes in the structure of plant-associated bacterial communities in the root zone towards the selection of assemblages that are adapted to abiotic stress, improve the resistance against stressors to promote health and drought tolerance of plants (Schmidt et al., 2014; Cherif et al., 2015). Variation in the distribution of bacteria was observed at endosphere, rhizosphere and the root surrounding soil compared to uncultivated soil associated with drought-sensitive pepper plant under desert farming conditions (*Capsicum annuum* L.) indicating a selective pressure determined by the plant activity on the structure of microbiome (Marasco et al., 2012). In a similar study, pepper plants inoculated with bacterial isolates from deserts exhibited a higher tolerance to water shortage, compared with control. Inoculation enhanced the root system (up to 40%), which improved plant ability to uptake water (Marasco et al., 2013). This study provides initial evidence that the nature of the interaction has limited level of specificity and that plant growth promoting bacteria (PGPB) determine resistance to water stress in plants others than the original isolation (Marasco et al., 2013). Bacterial microbiome of *Salicornia* plants grown under hypersaline ecosystems in Tunisia showed resistance to a wide set of abiotic stresses and were able to perform different plant growth promoting (PGP) activities and higher root colonization suggesting that the halophilic/halotolerant bacteria inhabiting salty and arid ecosystems have a potential to promote plant growth under salinity and drought condition (Mapelli et al., 2013).

Microbial communities below the ground level influence the selection on plant traits by mitigating the effects of abiotic stress on plant populations (Lau and Lennon, 2011). Manipulation of below-ground microbial communities showed that *Brassica rapa* grown in soils with simplified microbial communities were smaller, with reduced chlorophyll content, fewer flowers, and less fecund when compared with plant populations grown in association with more complex soil microbial communities (Lau and Lennon, 2011). Chamomile seedlings inoculated with three indigenous Gram-positive strains (*S. subrutilus* Wbn2-11, *B. subtilis* Co1-6, *P. polymyxa* Mc5Re-14) from Egypt and three Gram-negative strains (*P. fluorescens* L13-6-12, *S. rhizophila* P69, *S. plymuthica* 3Re4-18) from Europe revealed significant differences in the bacterial community structure. These differences clearly show a shift within the community structure. Moreover, *B. subtilis* Co1-6 and *P. polymyxa* Mc5Re-14 showed an enhancement of the bioactive secondary metabolite apigenin-7-*O*-glucoside. Inoculation of *Pseudomonas* sp. strain AKM-P6 and *P. putida* strain AKM-P7 enhanced the tolerance of sorghum and wheat seedlings to high temperature stress due to the synthesis of high-molecular weight proteins and also improved the levels of cellular metabolites (Ali et al., 2009, 2011). Hence, these studies indicate a new function of bacterial inoculants to interact with the plant microbiome as well as to influence the plant metabolome (Schmidt et al., 2014). Microbial diversity studies in native Egyptian desert soil in comparison to the agricultural soil, which was used more than 30 years for organic agriculture showed a significant difference in microbial community. *Bacillus*, *Paenibacillus* and Firmicutes were higher in field in comparison to desert soil but *Streptomyces* were antagonists from desert soil. On the other hand, several extremophilic bacteria disappeared from the soil after agricultural use. Bacterial communities in agricultural soil showed a higher diversity and a better ecosystem function for

plant health (Köberl et al., 2011, 2013; Ding et al., 2013). Effects of soil pH, nutrient concentration, salinity, and water content on bacterial diversity in soils collected from Mediterranean, semi-arid, and arid sites receiving approximately 400, 300, and 100 mm annual precipitation, respectively indicated that although soil bacterial abundance decreases with precipitation, bacterial diversity is independent of precipitation gradient. Furthermore, community composition was found to be unique to each ecosystem (Bachar et al., 2010).

The beneficial microbiome associated with roots and plant tissues alleviate plant stress by a variety of mechanisms (Rolli et al., 2014; Berg et al., 2013). Among them, PGPR can directly enhance micronutrient uptake and affect phytohormones homeostasis, or indirectly stimulate the plant immune system against phytopathogens (Balloi et al., 2010). PGP bacteria with 1-aminocyclopropane-1-carboxylate (ACC) deaminase enzyme (ACCd) can cleave the plant ethylene precursor ACC, thereby lowering the level of ethylene in stressed plants (Glick, 2004). Similarly, with an enhanced effect in drought-sensitive rootstock through a water stress-induced promotion, *Acinetobacter* and *Pseudomonas* enhanced shoot, leaf biomass and photosynthetic activity of drought challenged grapevines suggesting PGP activity as stress-dependent (Rolli et al., 2014). Several functional gene groups for stress protection, energy production, and cell motility were induced in *Stenotrophomonas rhizophila* DSM14405^T in response to salt or root extracts. Negative regulation of flagella-coding genes, up regulation of biofilm formation and alginate biosynthesis genes were identified as a single mechanism against salt shock (Alavi et al., 2013). Plant growth parameters were affected to varying degrees to *Azospirillum brasilense* and *Bacillus pumilus*, native arbuscular mycorrhizal (AM) fungi, and small quantities of compost, in highly eroded southern Sonoran Desert fields restored with three native leguminous trees. (Bashan et al., 2012).

PGPR are able to transcend the endodermis barrier, crossing from the root cortex to the vascular system, and subsequently thrive as endophytes in stem, leaves, tubers, and other organs (Kloepper et al., 1999; Gray and Smith, 2005; Compant et al., 2005). The extent of endophytic colonization of host plant organs and tissues reflects the ability of PGPR to selectively adapt to these specific ecological niches (Hallman et al., 1997; Gray and Smith, 2005). Epi and endophytic putative inflorescence colonization by *B. phytofirmans* strain PsJN in *Vitis vinifera* L. grown in nonsterile soil showed variation among plants for bacterial colonization of inflorescences. Whereas microscopic analysis revealed PsJN as a thriving endophyte in inflorescence organs after the colonization process (Compant et al., 2008). Colonization patterns of *V. vinifera* L. Cv. Chardonnay plantlets by *Burkholderia* sp. strain PsJN, showed chronological detection, first on root surfaces, then in root internal tissues, and finally in the fifth internode and the tissues of the fifth leaf. Furthermore, cell wall-degrading endoglucanase and endopolygalacturonase secreted by PsJN explained how the bacterium gains entry into root internal tissues (Compant et al., 2005). Ecology of date palm root endophytes from oases in the Tunisian Sahara showed bacteria rapidly cross-colonized the root tissues of different palm cultivars and *Arabidopsis*. Endophytes significantly increased the biomass exposed to drought stress indicating that date palm roots shape endophytic communities capable of promoting plant growth under drought, thereby contributing an essential ecological service to the entire oasis ecosystem (Cherif et al., 2015). Endophytic bacteria induce resistance to abiotic stress tolerance in plant species (Theocharis et al., 2012). At 4 °C, stress-related gene transcripts and metabolite levels increased faster and reached higher levels in *Burkholderia phytofirmans* PsJN-bacterized grapevine plantlets than in non-bacterized plants. The recorded changes are correlated with the tolerance to cold stress conferred by the presence of PsJN (Theocharis et al., 2012). Similarly, rice plants exhibited enhanced salt, drought and cold tolerance via symbiosis with Class 2 endophytes isolated from plants growing across moisture and salinity gradients. Under drought stress inoculation reduced water consumption, increased growth rate, yield and biomass. This indicates that symbiotic technology may be useful in mitigating impacts of climate change and expanding agricultural production onto marginal lands (Redman et al., 2011). A three-way mutualistic symbiosis involving a virus, a fungal endophyte, and a plant in conferring heat tolerance showed that when fungal isolates cured of the virus are unable to confer heat tolerance, but heat tolerance is restored after the virus is reintroduced. The virus-infected fungus confers heat tolerance not only to its native monocot host but also to a eudicot host, which suggests that the underlying mechanism involves pathways conserved between these groups of plants (Márquez et al., 2007).

1.3. Role of PGPR in drought stress

The role of microorganisms in plant growth, nutrient management and biocontrol activity is very well established. These beneficial microorganisms colonize the rhizosphere/endo-rhizosphere of plants and promote growth of the plants through various direct and indirect mechanisms (Grover et al., 2011). Furthermore, the role of microorganisms in management of biotic and abiotic stresses is gaining importance. The possible explanation for the mechanism of plant drought tolerance induced by rhizobacteria include: (1) production of phyto hormones like abscisic acid (ABA), gibberellic acid, cytokinins, and indole-3-acetic acid (IAA); (2) ACC deaminase to reduce the level of ethylene in the roots; (3) induced systemic tolerance by bacterial compounds; (4) bacterial exopolysaccharides (Yang et al., 2009; Dimkpa et al., 2009; Timmusk and Nevo, 2011; Kim et al., 2013; Timmusk et al., 2014) (Fig. 1). We therefore attempt to throw more light on the mechanisms that operate in microbial species that possess stress alleviating potential and their use in sustainable agriculture. This present review encompasses an overview of the current work reported on role of PGPR in helping plants to cope with drought stress.

2. Mechanisms of PGPR mediated drought stress tolerance

Several mechanisms have been proposed for PGPR mediated drought stress tolerance in plants. It includes phytohormonal activity, volatile compounds, alteration in root morphology, ACC deaminase activity, accumulation of osmolytes, EPS production, antioxidant defense and co-inoculations. The term Induced Systemic Tolerance (IST) has been coined to accommodate the microbial induced physical and chemical changes in plants, which result in enhanced tolerance to abiotic stresses (Yang et al., 2009).

2.1. Modification of phytohormonal activity in imparting drought tolerance in plants

Phytohormones such as IAA, gibberellins, ethylene, abscisic acid and cytokinins are produced by plants, which are important for their growth and development (Barea and Brown, 1974; Frankenberger and Arshad, 1995; Teale et al., 2006; Egamberdieva, 2013). Phytohormones play a role in plants to abiotic stress to escape or survive stressful conditions (Skirycz and Inze, 2010; Fahad et al., 2015). Furthermore, PGPRs are able to synthesize phytohormones that stimulate plant cell growth and division to become tolerant against environmental stresses (Glick and Pasternak, 2003).

Physiologically most active auxin in plant growth and development is IAA. Various plant species inoculated with IAA producing bacteria increased root growth and/or enhanced formation of lateral roots and roots hairs (Dimkpa et al., 2009) thus increasing

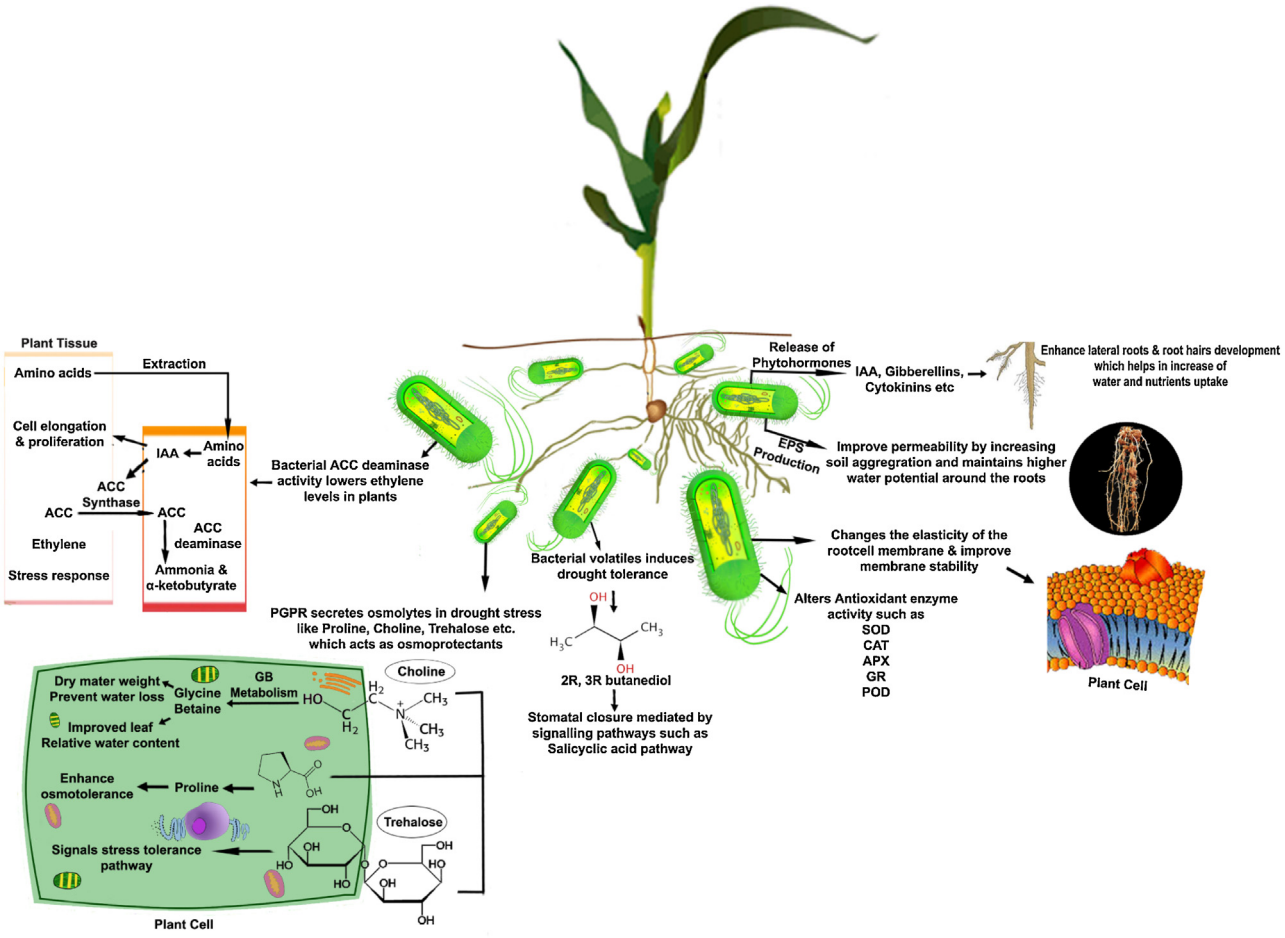
Plant Tissue
Amino acids
Extraction
Cell elongation & proliferation
IAA
Amino acids
ACC Synthase
ACC
ACC
ACC deaminase
Ethylene
Stress response
Ammonia & α-ketobutyrate
Bacterial ACC deaminase activity lowers ethylene levels in plants
Release of Phytohormones
IAA, Gibberellins, Cytokinins etc
Enhance lateral roots & root hairs development which helps in increase of water and nutrients uptake
EPS Production
Improve permeability by increasing soil aggregration and maintains higher water potential around the roots
Changes the elasticity of the rootcell membrane & improve membrane stability
Alters Antioxidant enzyme activity such as SOD CAT APX GR POD
Plant Cell
Bacterial volatiles induces drought tolerance
2R, 3R butanediol
Stomatal closure mediated by signalling pathways such as Salicyclic acid pathway
PGPR secretes osmolytes in drought stress like Proline, Choline, Trehalose etc. which acts as osmoprotectants
Dry mater weight
Prevent water loss
Glycine Betaine
GB Metabolism
Choline
Improved leaf Relative water content
Enhance osmotolerance
Proline
Trehalose
Signals stress tolerance pathway
Plant Cell

Fig. 1. Mechanism of plant drought tolerance induced by plant growth promoting rhizobacteria.

water and nutrient uptake (Mantelin and Touraine, 2004), helping plants to cope with water deficit (Egamberdieva and Kucharova, 2009). IAA producing *Azospirillum* enhanced plant's tolerance to drought stress (Dimkpa et al., 2009). Bacterial hormone production and their ability to stimulate endogenous hormones plays the key role in enhancing tolerance (Dobbelaere et al., 1999; Cassan et al., 2001). *A. brasilense* producing nitric oxide, a small diffusible gas act as a signaling molecule in IAA inducing pathway and helps in adventitious root development in tomato plants (Creus et al., 2005; Molina-Favero et al., 2008). Similarly, inoculation with *A. brasilense* Cd increased root projection area, specific root length and specific root area, as compared with non-inoculated controls of common bean (*Phaseolus vulgaris* L.) under drought stress (German et al., 2000). The effects of *A. brasilense* Cd on root morphology are related to its ability to produce phytohormones, mainly auxins (Dimkpa et al., 2009).

In case of maize seedlings, inoculation with *A. brasilense* improved relative and absolute water contents compared to non-inoculated plants under drought stress. Bacterial treatment dropped the water potential but increased the root growth, biomass, foliar area, and proline accumulation in leaves and roots. These effects were more significant at 75% reduction in water supply, compared to 50% reduction (Casanovas et al., 2002). Inoculation of *A. brasilense* Sp245 in wheat (*Triticum aestivum*) under drought stress resulted in better grain yield and higher mineral quality (Mg, K and Ca), with improved relative and absolute water content, water potential, apoplastic water fraction and lower volumetric cell wall elasticity suggesting that, in addition to better water status, an 'elastic adjustment' is crucial in increased drought tolerance in plants (Creus et al., 2004). Similarly, *Azospirillum*-wheat association induced decrease in leaf water potential and increase in leaf water content, which was attributed to the production of plant hormones such as IAA by the bacteria that enhanced root growth and formation of lateral roots their by increasing uptake of water and nutrients under drought stress (Arzanesh et al., 2011). PGPR *B. thuringiensis* helped *Lavandula dentate* plants to grow under drought conditions due to the production of IAA by the bacterium which improved nutrition, physiology, and metabolic activities of plant (Armada et al., 2014). Soybean plants inoculated with gibberellins secreting rhizobacterium *P. putida* H-2–3 improved plant growth under drought conditions (Sang-Mo et al., 2014). Production of ABA and gibberellins by *Azospirillum lipoferum* alleviated drought stress in maize plants (Cohen et al., 2009). Cellular dehydration induced biosynthesis of ABA, a stress hormone during water deficit condition (Kaushal and Wani, 2015). ABA is involved in water loss regulation by controlling stomatal closure and stress signal transduction pathways (Yamaguchi-Shinozaki and Shinozaki, 1994). *Arabidopsis* plants inoculated with *A. brasilense* Sp245 had elevated levels of ABA compared to non-inoculated plants (Cohen et al., 2008). PGPR *Phyllobacterium brassicacearum* strain STM196, isolated from the rhizosphere of *Brassica napus* enhanced osmotic stress tolerance in inoculated *Arabidopsis* plants by elevating ABA content, leading to decreased leaf transpiration (Bresson et al., 2013). Inoculation of *Platycladus orientalis* seedlings with cytokinin producing PGPR (*Bacillus subtilis*) elevated the levels of ABA in

Table 1
PGPR phytohormonal activity in imparting drought tolerance in plants.

PGPR	Plant species	Effect	Reference
A. brasilense	Tomato	Nitric oxide as a signaling molecule in IAA induced pathway which enhanced lateral root and root hair development	Creus et al. (2005) Molina-Favero et al. (2008)
Azospirillum lipoferum	Maize	Gibberellins increased ABA levels and alleviated drought stress	Cohen et al. (2009)
Azospirillum sp.	Wheat	IAA enhanced root growth, lateral roots formation and increased uptake of water and nutrients under drought stress	Arzanesh et al. (2011)
Phyllobacterium brassicacearum strain STM196	*Arabidopsis*	Enhanced ABA content resulted in decreased leaf transpiration	Bresson et al. (2013)
Bacillus subtilis	*Platycladus orientalis*	Cytokinin production by PGPR elevated ABA levels in shoots and increased the stomatal conductance	Liu et al. (2013)
P. putida H-2–3	Soybean	Secretion of gibberellins by *P.putida* improved plant growth	Sang-Mo et al. (2014)
B. thuringiensis	*Lavandula dentate*	IAA resulted in higher K-content, proline and decreased the glutathione reductase (GR) and ascorbate peroxidase (APX)	Armada et al. (2014)
Rhizobium leguminosarum (LR-30), *Mesorhizobium ciceri* (CR-30 and CR-39), and *Rhizobium phaseoli* (MR-2)	Wheat	IAA produced by the consortia improved the growth, biomass and drought tolerance index	Hussain et al. (2014)

shoots and increased the stomatal conductance conferring drought stress resistance (Liu et al. 2013) (Table 1).

2.2. Role of volatiles in inducing drought tolerance

Induction of volatiles takes place when plants are exposed to a multitude of stresses (Loreto and Schnitzler, 2010; Holopainen and Gershenzon, 2010). These stress-induced volatiles serve as signals for developing priming and systemic responses within the same and in neighboring plants (Heil and Silva Bueno, 2007; Choudhary et al., 2008; Niinemets, 2010). Bacterial priming with *Bacillus thuringiensis* AZP2 in wheat seedlings under drought stress resulted in enhanced plant biomass and five-fold higher survival under severe drought due to significant reduction of volatile emissions and higher photosynthesis (Timmusk et al., 2014). This suggests that bacterial inoculation improved plant stress tolerance (Timmusk et al., 2014). Volatiles are promising candidates for rapid non-invasive technique to assess crop drought stress and its mitigation during stress development (Timmusk et al., 2014). Root colonization with *Pseudomonas chlororaphis* O6 prevents water loss by stomatal closure mediated by 2R, 3R-butanediol, a volatile metabolite produced by *P. chlororaphis* O6, whereas, bacteria deficient in 2R, 3R-butanediol production showed no induction of drought tolerance. Microbial volatile 2R, 3R-butanediol helps in inducing resistance to drought stress in *Arabidopsis* (Cho et al., 2008). Further, *Arabidopsis* mutant lines indicated that induced drought tolerance required the salicylic acid (SA), ethylene and jasmonic acid-signaling pathways. Both induced drought tolerance and stomatal closure were dependent on Aba-1 and OST-1 kinase (Cho et al., 2008). Increase in free SA in *P. chlororaphis* O6-colonized plants under drought stress and after 2R, 3R-butanediol treatment suggests the primary role of SA signaling in inducing drought tolerance. Bacterial volatile 2R, 3R-butanediol was a major determinant in inducing resistance to drought in *Arabidopsis* through an SA-dependent mechanism (Cho et al., 2008).

2.3. PGPR alter root morphology under drought stress

Plant's physiological status is regulated by cell membranes and rhizobacteria can influence processes taking place at these sites. *A. brasilense* reduced membrane potentials in wheat seedlings and phospholipid content in the cell membranes of cowpea due to the changes in proton efflux activities (Bashan et al., 1992). Water deficit changes the phospholipid composition in the root, increases phosphatidylcholine and reduces phosphatidylethanolamine (Sueldo et al., 1996), but inoculation with *Azospirillum* prevented these changes in wheat seedlings, though higher phosphatidylcholine and lower phosphatidylethanolamine unsaturation occurred (Pereyra et al., 2006). Bacteria mediated changes in the elasticity of the root cell membranes is one of the first steps towards enhanced tolerance to water deficiency (Dimkpa et al., 2009). PGPR improves the stability of plant cell membranes by activating the antioxidant defense system, enhancing drought tolerance in plants (Gusain et al., 2015).

2.4. Role of ACC deaminase producing rhizobacteria in drought stress tolerance

Plant activities are regulated by ethylene levels and the biosynthesis of ethylene is regulated by biotic and abiotic stresses (Hardoim et al., 2008). In the biosynthetic pathway of ethylene, S-adenosylmethionine (S-AdoMet) is converted by 1-aminocyclopropane-1-carboxylate synthase (ACS) to 1-aminocyclopropane-1-carboxylate (ACC), the immediate precursor of ethylene. Under stress conditions, the plant hormone ethylene endogenously regulates plant homoeostasis resulting in reduced root and shoot growth. Plant ACC is sequestered and degraded by ACC deaminase producing bacteria to supply nitrogen and energy. Furthermore, by removing ACC the bacteria reduce the deleterious effect of ethylene, ameliorating plant stress and promoting plant growth (Glick, 2005). ACC deaminase producing PGPR *Achromobacter piechaudii* ARV8 significantly increased the fresh and dry weights of both tomato and pepper seedlings and reduced the ethylene production under drought stress (Mayak et al., 2004). Rhizobacteria populating the sites where water is limited with repeated dry periods are likely to be more stress adapting and promote plant growth than those bacteria isolated from the sites where water sources are abundant (Mayak et al., 2004). The seedlings treated with *A. piechaudii* ARV8, a bacterial strain isolated from an arid site, were significantly better in growth than the seedlings treated with a bacterium, *P. putida* GR12-2 that was originally isolated from the rhizosphere of grasses in the high Canadian Arctic areas where water is abundant (Lifshitz et al., 1986).

Inoculation of pea plants with the ACC deaminase producing *Variovorax paradoxus* 5C-2 were more pronounced and consistent under soil drying condition (Dodd et al., 2005). Plants inoculated

Table 2
ACC deaminase producing PGPR in mitigation of drought stress in plants.

PGPR	Plant species	Effect	Reference
Achromobacter piechaudii ARV8	Tomato and Pepper	Reduced ethylene production and increased fresh and dry weight	Mayak et al. (2004)
Variovorax paradoxus 5C-2	Pea	Increased nodulation, seed yield, seed number and seed nitrogen content	Dodd et al. (2005)
Pseudomonas fluorescens biotype G (ACC-5)	*Pisum sativum*	Induced longer roots and increased uptake of water	Zahir et al. (2008)
V. paradoxus 5C-2	Pea	Increase in xylem abscisic acid, higher nodulation, growth, yield and water-use efficiency	Belimov et al. (2009)
ACC deaminase producing rhizobacteria	Wheat	Increased root-shoot length, biomass and lateral root number	Shakir et al. (2012)
Consortia of *Bacillus* isolate 23-B and *Pseudomonas* 6-P with *Mesorhizobium ciceris*	*Cicer arietinum*	Higher proline concentration, improved germination, root and shoot length and fresh weight of the seedlings	Sharma and Khanna (2013)
Bacillus licheniformis K11	Pepper	Higher expression of stress genes Cadhn, VA, sHSP and CaPR-10	Hui and Kim (2013)
Bacillus thuringiensis AZP2	Wheat	Reduction of volatile emissions and higher photosynthesis	Timmusk et al. (2014)

with ACC deaminase producing bacterium gave more seed yield, seed number and seed nitrogen accumulation and restoring nodulation which was depressed in drought stress conditions (Dodd et al., 2005). ACC deaminase producing bacteria eliminated the effects of drought stress on growth, yield, and ripening of pea in both pot and field trials (Arshad et al., 2008). Inoculation of *Pisum sativum* with ACC deaminase producing *Pseudomonas fluorescens* biotype G (ACC-5) induced longer roots, which led to an increased uptake of water from soil under drought stress (Zahir et al., 2008). Inoculation with *V. paradoxus* 5C-2 improved growth, yield and water-use efficiency of droughted peas (Belimov et al., 2009). Systemic effects of *V. paradoxus* 5C-2 showed soil drying-induced increase of xylem abscisic acid (ABA) and an attenuated soil drying-induced increase of xylem ACC (Dodd et al., 2005). Increased nodulation by symbiotic nitrogen-fixing bacteria prevented drought-induced decrease in nodulation and seed nitrogen content. Successful deployment of bacteria in the rhizosphere increased yield and nutritive value of plants in dry soil, via both local and systemic hormone signaling. Such bacteria provide an easily realized, economic means of sustaining crop yields in dryland agriculture (Belimov et al., 2009). Axenic studies showed that inoculation with ACC deaminase producing rhizobacteria increased root–shoot length, root-shoot mass and lateral root number of wheat plants compared to control. Better development of roots helped plants to acquire water and nutrients resulting in improved growth and yield under drought stress (Shakir et al., 2012). Co-inoculation of ACC deaminase producing *Bacillus* isolate 23-B and *Pseudomonas* 6-P with *Mesorhizobium ciceris* for mitigation of drought stress and plant growth promotion under axenic conditions on *Cicer arietinum* varieties (*Kabuli* L-552 and *Desi* GPF-2) significantly improved germination, root and shoot length and fresh weight of chickpea seedlings under osmotic potential up to 0.4 MPa over uninoculated control. Proline content was higher in PGPR treated varieties under water stress. Among the treatments co-inoculation of 23-B with *Mesorhizobium* was efficient under drought stress (Sharma and Khanna, 2013). Similarly, pepper inoculated with ACC deaminase producing *Bacillus licheniformis* K11 alleviated drought stress and six differentially expressed stress proteins were identified by 2D-PAGE (Hui and Kim, 2013) (Table 2).

2.5. Osmolytes in imparting drought tolerance in plants

Plants adaptation to drought stress is associated with metabolic adjustments that lead to the accumulation of several compatible solute/osmolytes like proline, sugars, polyamines, betaines, quaternary ammonium compounds, polyhydric alcohols and other amino acids and water stress proteins like dehydrins (Yancey et al., 1982; Close, 1996). PGPR secrete osmolytes in response to drought stress, which act synergistically with plant-produced osmolytes and stimulate plant growth (Paul et al., 2008). PGPR *Pseudomonas putida* GAP-P45 inoculation improved plant biomass, relative water content and leaf water potential by accumulation of proline in maize plants exposed to drought stress (Sandhya et al., 2010). Inoculating plants with PGPR adds up to the existing concentrations of proline, a sizeable quantity of proline increased when maize plants were inoculated with *P. fluorescens* under drought stress (Ansary et al., 2012). Drought tolerance of *L. dentate* showed that PGPR *B. thuringiensis* (Bt) inoculation enhanced shoot proline accumulation when compared to control plants under drought stress (Armada et al., 2014). Increased proline content due to up regulation of proline biosynthesis pathway keeps proline in high levels to help in maintaining cell water status, protects membranes and proteins from stress (Sandhya et al., 2010). Similarly, tomato (*Lycopersicon esculentum* Mill) cv. Anakha treated with phosphate solubilizing bacteria (PSB) (*Bacillus polymyxa*) secreted excess proline to cope up with the drought condition (Shintu and Jayaram, 2015). PGPR consortia containing *Pseudomonas jessenii* R62, *Pseudomonas synxantha* R81 and *Arthrobacter nitroguajacolicus* strainYB3, strain YB5 enhanced plant growth in Sahbhagi (drought tolerance) and IR-64 (drought sensitive) cultivars of rice (*Oryza sativa* L.). Higher proline accumulation in inoculated plants indicate higher plant tolerance to water stress (Gusain et al., 2015). In severe drought stress both the consortia treated varieties showed higher proline in almost similar way, the attribute might differentiate the tolerant and sensitive varieties of rice suggesting the vital role of proline as an osmoregulatory solute in plants (Gusain et al., 2015). Inoculation of maize plant with PGPR *P. putida* GAP-P45 (Sandhya et al., 2010) and *A. lipoferum* (Bano et al., 2013) improved plant growth through accumulation of free amino acids and soluble sugars compared to non-treated plants under drought stress.

Trehalose, a non-reducing disaccharide acts as osmoprotectant by stabilizing dehydrated enzymes and membranes; its biosynthesis imparts osmoprotection (Yang et al., 2010). Enhanced drought tolerance was observed in *P. vulgaris* plants inoculated with *Rhizobium etli* overexpressing trehalose-6-phosphate synthase gene compared with plants inoculated with the wild strain (Suarez et al., 2008). Macro array analysis of 7200 expressed sequence tags from nodules of plants inoculated with the strain overexpressing trehalose-6-phosphate synthase gene revealed upregulation of genes involved in stress tolerance, carbon and nitrogen metabolism, suggesting a signaling mechanism for trehalose (Suarez et al., 2008). It is well established that trehalose

Table 3
PGPR enhances osmolytes accumulation in imparting drought tolerance in plants.

PGPR	Plant species	Effect	Reference
Pseudomonas putida GAP-P45	Maize	Accumulation of proline improved plant biomass, relative water content and leaf water potential	Sandhya et al. (2010)
P. fluorescens	Maize	Increased proline, abscisic acid, auxin, gibberelline and cytokinin content improved plant growth	Ansary et al. (2012)
B. thuringiensis	*Lavandula dentate*	IAA induced higher proline and K-content, improved nutritional, physiological, and metabolic activities and decreased glutathione reductase (GR) and ascorbate peroxidase (APX) activity	Armada et al. (2014)
Bacillus polymyxa	*Lycopersicon esculentum*	Proline accumulation improved the physiological and biochemical parameters of plants	Shintu and Jayaram (2015)
Consortia containing *P. jessenii*, R62, *P. synxantha*, R81 and *A. nitroguajacolicus* strainYB3, strain YB5	*Oryza sativa*	Accumulation of proline maintained osmotic adjustment and improved plant growth	Gusain et al. (2015)
Azospirillum lipoferum	Maize	Improved plant growth through accumulation of free amino acids and soluble sugars	Bano et al. (2013)
Rhizobium etli overexpressing trehalose-6-phosphate synthase gene	*Phaseolus vulgaris*	Trehalose act as a signaling molecule in upregulation of genes involved in stress tolerance, carbon and nitrogen metabolism	Suarez et al. (2008)
A. brasilense overexpressing trehalose biosynthesis gene	Maize	Trehalose translocated to the maize roots and triggered stress tolerance pathways in the plant	Rodriguez et al. (2009)
Bacillus subtilis GB03	*Arabidopsis*	Expression of *PEAMT* gene resulted in elevated metabolic level of choline together with GB in osmotically stressed plants and improved leaf RWC and dry DMW	Zhang et al. (2010)
Klebsiella variicola F2, *Pseudomonas fluorescens* YX2 and *Raoultella planticola* YL2	Maize	Accumulation of choline and GB and improved leaf RWC and DMW	Gou et al. (2015)
Azoapirillum brasilense Az39	Rice	Cadaverine production by PGPR improved root growth and mitigated osmotic stress	Cassan et al. (2009)

plays an important role as a signaling molecule in plants (Paul et al., 2008). Similar effects were observed in maize plants inoculated with *A. brasilense* overexpressing trehalose biosynthesis gene (Rodriguez et al., 2009). Inoculation imparted drought tolerance in maize and significantly increased the plant biomass. It is hypothesized from the study that very small amounts of trehalose translocated to the maize roots and signal stress tolerance pathways in the plant. Thus, trehalose metabolism in PGPR is key for signaling plant growth, yield, and adaptation to abiotic stress, and its manipulation has a major agronomical impact on plants (Rodriguez et al., 2009) (Table 3).

Choline plays a critical role in plant stress resistance, mainly for enhancing glycine betaine (GB) synthesis and accumulation (Zeisel, 2006; Zhang et al., 2010). Evident reports on induced role of *B. subtilis* GB03 in *Arabidopsis* (Zhang et al., 2010) and *Klebsiella variicola* F2, *P. fluorescens* YX2 and *Raoultella planticola* YL2 in maize showed enhancements in biosynthesis and accumulation of choline as a precursor in GB metabolism, resulting in the accumulation of GB thereby improving leaf relative water content (RWC) and dry mater weight (DMW) (Glick et al., 2007; Zhang et al., 2010; Gou et al., 2015). The increased content of choline in drought stressed maize plants supplied more nutrition as a food additive (Zeisel, 2006; Zhang et al., 2010). The relative expression of *PEAMT* gene induced in *Arabidopsis* by *B. subtilis* GB03 were almost 3-fold as compared with uninoculated plants under osmotic stress, resulting in elevated metabolic level of choline together with GB in osmotically stressed plants (Zhang et al., 2010). Enhanced accumulation of solutes such as GB was induced by PGPR stains under stress conditions that regulated plant stress responses by preventing water loss caused by osmotic stress (Nadeem et al., 2010; Bashan et al., 2014). Similarly, osmotic stressed plants inoculated with PGPR stains such as *B. subtilis* GB03 and *Pseudomonas* spp. accumulated significantly higher GB than those in plants without inoculation (Sandhya et al., 2010), might be attributed to up-regulation of GB biosynthesis pathway by enhancing some key enzymes gene expression such as *PEAMT* (Zhang et al., 2010). Similarly, polyamines are considered as plant growth regulating compounds among them, cadaverine was correlated with root growth promotion or osmotic stress mitigation in plants. Role of cadaverine producing *A. brasilense* Az39 promoted root growth and helped to mitigate osmotic stress in rice seedlings Cassan et al. (2009).

2.6. Exopolysaccharide (EPS) production by rhizobacteria and alleviation of drought stress

Drought stress can make physico–chemical and biological properties of soil unsuitable for soil microbial activity and crop yield. Water availability controls the production and consumption of protein and polysaccharides by the bacteria (Roberson and Firestone, 1992) and thus indirectly influences soil structure. Exopolysaccharide (EPS) production by microbes protects them from inhospitable conditions and enables their survival. Capsular material of *A. brasilense* Sp245 contain high molecular weight carbohydrate complexes (lipopolysaccharide–protein (LP) complex and polysaccharide–lipid (PL) complex) responsible for protection under extreme conditions like desiccation. Addition of these complexes to a suspension of decapsulated cells of *A. brasilense* Sp245 significantly enhanced survival under drought stress (Konnova et al., 2001). The EPS released into soil as capsular and slime materials by soil microbes can be adsorbed by clay surfaces due to cation bridges, hydrogen bonding, Van der Waals forces, and anion adsorption mechanisms thus forming a protective capsule around soil aggregates (Tisdall and Oades, 1982; Sandhya et al., 2009). EPS provides a microenvironment that holds water and dries up more slowly than the surrounding environment thus protecting the bacteria and plant roots against desiccation (Hepper, 1975). Production

of EPS by bacteria has been shown to improve permeability by increasing soil aggregation and maintaining higher water potential around the roots, thereby increasing in the uptake of nutrients by plant with an increase in plant growth and protection from drought stress (Miller and Wood, 1996; Alami et al., 2000; Selvakumar et al., 2012). Plants treated with EPS-producing bacteria display increased resistance to water stress (Bensalim et al., 1998). Significant increase in root adhering soil per root tissue (RAS/RT) ratio was observed in sunflower rhizosphere inoculated with the EPS-producing rhizobial strain YAS34 under drought conditions (Alami et al., 2000). Inoculation of *Pseudomonas* sp. strain GAP-P45 increased the survival, plant biomass and RAS/RT of sunflower seedlings subjected to drought stress. The inoculated rhizobacteria could efficiently colonize the root adhering soil, rhizoplane and increase the percentage of stable soil aggregates. Better aggregation of RAS leads to increased uptake of water and nutrients from rhizosphere soil, thus ensuring plant growth and survival under drought stress (Sandhya et al., 2009). Seed bacterization of maize with EPS-producing bacterial strains *Proteus penneri* (Pp1), *Pseudomonas aeruginosa* (Pa2) and *Alcaligenes faecalis* (AF3) along with their respective EPS improved soil moisture contents, plant biomass, root and shoot length and leaf area. Under drought stress, the inoculated plants showed increase in relative water content, protein, sugar and proline content and the activities of antioxidant enzymes were decreased (Naseem and Bano, 2014). Inoculation of catalase and exopolysaccharides producing *Rhizobium leguminosarum* (LR-30), *Mesorhizobium ciceri* (CR-30 and CR-39) and *Rhizobium phaseoli* (MR-2) showed beneficial interaction to wheat (non-legume) under drought stress. Inoculation improved the growth, biomass and drought tolerance index of the wheat seedlings under poly ethylene glycol (PEG) 6000 simulated drought. Isolates produced indole acetic acid which enhanced the root length of the seedlings to dilute the drought stress (Hussain et al., 2014).

2.7. Altering antioxidant defense system

Exposure of plants to drought stress leads to the generation of reactive oxygen species (ROS), including superoxide anion radicals (O_2^-), hydrogen peroxide (H_2O_2), hydroxyl radicals (OH), singlet oxygen (O_{12}) and alkoxy radicals (RO). ROS react with proteins, lipids and deoxyribonucleic acid causing oxidative damage and impairing the normal functions of plant cell. In order to over-come these effects, plants develop antioxidant defense systems comprising both enzymatic and non-enzymatic components that serve to prevent ROS accumulation and alleviate the oxidative damage occurring during drought stress (Miller et al., 2010). Enzymatic components include superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APX), and glutathione reductase (GR). Non-enzymatic components contain cysteine, glutathione and ascorbic acid (Kaushal and Wani, 2015).

Maize plants inoculated with five drought tolerant plant growth promoting *Pseudomonas* spp. strains namely *P. entomophila*, *P. stutzeri*, *P. putida*, *P. syringae*, and *P. montelli* subjected to drought stress showed significantly lower activity of antioxidant enzymes as compared to uninoculated plants (Sandhya et al., 2010). Similarly, maize plants inoculated with *Bacillus* species developed protection against drought stress by reducing activity of the antioxidant enzymes APX and Glutathione peroxidase (GPX) (Vardharajula et al., 2011). In field studies basil plants (*Ocimum basilicum* L.) treated with *Pseudomonas* sp. under drought stress, significantly increased the CAT enzyme activity, similarly when treated with microbial consortia containing *Pseudomonades* sp., *Bacillus lentus* and *A. brasilense* highest activity of GPX and APX was observed (Heidari and Golpayegani, 2011). Decreased activity of APX, CAT and GPX enzymes was reported in maize plants inoculated with EPS-producing bacteria conferring stress tolerance to plants (Naseem and Bano, 2014). Effectiveness of autochthonous PGPR *B. thuringiensis* (Bt) in *Lavandula dentata* and *Salvia officinalis* under drought conditions promoted growth and drought avoidance by depressing stomatal conductance and decrease of glutathione reductase (GR) and ascorbate peroxidase (APX) activity (Armada et al., 2014). PGPRs, *P. jessenii* R62, *P. synxantha* R81 and *A. nitroguajacolicus* strainYB3 and strain YB5 used as consortia's enhanced plant growth and induction of stress related enzymes (SOD, CAT, peroxidase (POD), APX and lower level of H_2O_2, malondialdehyde (MDA)) in Sahbhagi (drought tolerance) and IR-64 (drought sensitive) cultivars of rice (*O. sativa* L.) under drought stress compared to control (Gusain et al., 2015). These studies provide evidence for a beneficial effect of PGPRs application in enhancing drought tolerance of plants by altering the antioxidants activity under water deficit conditions (Gusain et al., 2015).

2.8. Molecular studies in alleviation of drought stress by PGPR

Gene expression studies are a powerful tool to understand and compare the "holistic" responses of an organism to their environment (Karen et al., 2010). The transcriptome consists of the entire set of transcripts that are expressed with in a cell or organism at a particular developmental stage or under various environmental conditions. There are various technologies for assaying the transcriptome including hybridization-based microarrays to RNA sequencing (Trewavas, 2006; Wang et al., 2009). Gene expression by drought stress were recently characterized using molecular approaches (Kandasamy et al., 2009; Yuwono et al., 2005), their physiological roles with respect to tolerance induced by PGPR.

At the transcriptional level, PGPR enhanced plant tolerance to drought was observed with inoculation of PGPR *Paenibacillus polymyxa* B2, which enhanced drought tolerance of *Arabidopsis thaliana*. RNA display showed that an mRNA transcription of a drought-response gene, *EARLY RESPONSE TO DEHYDRATION 15* (*ERD15*) was augmented in inoculated plants compared to uninoculated controls (Timmusk and Wagner, 1999). Using 2-D polyacrylamide gel electrophoresis (2D-PAGE) and differential display polymerase chain reaction (DD-PCR), six differentially expressed stress proteins were identified in pepper plants inoculated with *B. licheniformis* K11 under drought stress. Among the stress proteins, specific genes of Cadhn, VA, sHSP and CaPR-10 showed more than a 1.5-fold increase in treated plants compared to control (Lim and Kim, 2013). Using Real-Time PCR (RT-PCR), upregulation of stress related genes APX1, SAMS1, and HSP17.8 in the leaves of wheat were identified and increased activity of enzymes involved in the plant ascorbate–glutathione redox cycle conferring drought tolerance in wheat when priming with *Bacillus amyloliquefaciens* 5113 and *A. brasilense* NO40 alleviating the deleterious effect of drought stress (Kasim et al., 2013). Using microarray analysis, a set of drought signaling response genes were down-regulated in the *P. chlororaphis* O6-colonized *A. thaliana* compared to those without bacterial treatment under drought stress. Transcripts of the jasmonic acid-marker genes, *VSP1* and *pdf-1.2*, salicylic acid regulated gene, *PR-1* and the ethylene-response gene, *HEL*, were up-regulated in colonized plants, but differed in their responsiveness to drought stress (Cho et al., 2013). Using Illumina sequencing (HiSeq 2000 system) the effects of the association between the diazotroph *Gluconacetobacter diazotrophicus* PAL5 and sugarcane cv. SP70-1143 under drought stress concluded that bacterial inoculation activated the ABA-dependent signaling genes conferring drought resistance in sugar cane cv. SP70-1143 Vargas et al. (2014) (Table 4).

2.9. Co-inoculation of PGPR for alleviation of drought stress

In addition to single strains of PGPR, its combination with either mycorrhizal fungi or *Rhizobium* elicits plant drought tol-

Table 4
Induction of drought responsive genes in plants by PGPR.

PGPR	Plant species	Drought responsive genes	Reference
Paenibacillus polymyxa B2	*Arabidopsis thaliana*	Induction of *EARLY RESPONSE TO DEHYDRATION 15 (ERD15)*	Timmusk and Wagner (1999)
B. licheniformis K11	Pepper	Inoculation increased stress protein genes Cadhn, VA, sHSP and CaPR-10	Lim and Kim (2013)
Bacillus amyloliquefaciens 5113 and *Azospirillum brasilense* NO40	Wheat	Upregulation of stress related genes APX1, SAMS1, and HSP17.8	Kasim et al. (2013)
Pseudomonas chlororaphis O6	*Arabidopsis thaliana*	Transcripts of the jasmonic acid-marker genes, *VSP1* and *pdf-1.2*, salicylic acid regulated gene, *PR-1*, and ethylene-response gene, *HEL*, were up-regulated in colonized plants	Cho et al. (2013)
Gluconacetobacter diazotrophicus PAL5	Sugarcane	Inoculation activated the ABA-dependent signaling genes conferring drought resistance	Vargas et al. (2014)

erance (Wang et al., 2012). Co-inoculation of common bean (*P. vulgaris* L.) with *Rhizobium tropici*-CIAT 899, *P. polymyxa*-DSM36 and *P. polymyxa*-Loutit strains resulted in greater growth compared to inoculation with *Rhizobium* alone. Furthermore, co-inoculation exhibited greater nodulation (number and biomass) and nitrogen content compared to drought-stressed plants inoculated with only *Rhizobium* (Figueiredo et al., 2008). PGPR strain *Pseudomonas mendocina* Palleroni and an arbuscular mycorrhizal (AM) fungus (either *Glomus intraradices* or *Glomus mosseae*) significantly enhanced the root phosphatase activity; and the proline accumulation and the activities of NR, POD and CAT in the lettuce leaves under moderate and severe drought stress (Kohler et al., 2008). Further co-inoculation of wheat plants with *Azotobacter chrocoocum* (E1) and *Pseudomonas* sp. (E2) alleviated drought stress through increased anatomical changes such as thickness of epidermis, ground, mesophyll and phloem tissues, diameter of xylem vessel and dimensions of vascular bundles of the root system, whereas water deficit levels (75, 50 and 25% field capacity) decreased the anatomical values of the un-inoculated wheat cultivars (El-Afry et al., 2012). Microbial consortium containing PGPR *Bacillus cereus* AR156, *B. subtilis* SM21 and *Serratia* sp. XY21 termed as BBS improved drought tolerance in cucumber plants. After withholding watering for 13 days, BBS treated plants exhibited darker green leaves with lighter wilt symptoms, decreased the leaf mono dehydroascorbate content and relative electrical conductivity, increased the leaf proline and chlorophyll content and root recovery intension in cucumber plants under drought stress. In comparison with control, the BBS treatment enhanced the SOD activity and mitigated the drought-triggered down-regulation of the genes cAPX, rbcL and rbcS encoding cytosolic ascorbate peroxidase and ribulose-1,5-bisphosphate carboxy/oxygenase (Rubisco) large and small subunits, respectively, in cucumber leaves (Wang et al. 2012). Microbial consortia consisting of EPS producing bacterial strains *P. penneri* (Pp1), *P. aeruginosa* (Pa2) and *A. faecalis* (AF3) showed greater potential to drought tolerance in maize compared to single PGPR strains (Naseem and Bano, 2014). PGPRs consortia alleviated drought stress in rice plants by reducing oxidative damage and accumulation of proline in rice plants grown under drought there by improved the plant growth (Gusain et al. 2015).

3. Future research

Agriculture is considered as most vulnerable sectors to climate-change. Exploiting plant-microbe interaction is a relevant approach to increase food production for the growing population in the current scenario of climate change. The future research needs to be in developing efficient microbial formulation for boosting plant performance under drought stress that substantially reduces the use of chemical fertilizers and pesticides. The research should focus on to isolate indigenous PGPR from the stress-affected soils that could be used as bioinoculants for crops grown in stressed ecosystems (Kaushal and Wani, 2015).

Many of the mechanisms underlying plant-microbe interactions in the rhizosphere are poorly understood. Difficulties rely mainly on profiling the great array of processes involved in microbial communities. Understanding this signal crosstalk is fundamental to optimize plant adaptation mechanisms and to improve the ability of soil microbes for stress alleviation in crops. A plethora of molecular techniques is becoming available, and is currently being applied to define the molecular bases of the plant-microbiome interactions (Barea, 2015).

Better understanding of what makes a beneficial PGPR interaction with plant would provide an important insight to better handle microbes. Despite the recent progress and perspectives highlighted on microbial mediated drought tolerance in plants, we are still at the beginning of our understanding of PGPR mechanisms imparting drought tolerance in plants. Nevertheless, current progress in the area conveys that future research has great potential to give new insights for sustainable food production.

4. Conclusion

Drought stress is a severe environmental constraint to agricultural productivity. PGPR plays an important role in conferring resistance and adaptation of plants to drought stresses and have the potential role in solving future food security issues. The interaction between plant and PGPR under drought conditions affects not only the plant but also changes the soil properties. The mechanisms elicited by PGPR such as triggering osmotic response and induction of novel genes play a vital role in ensuring plant survival under drought stress. The development of drought tolerant crop varieties through genetic engineering and plant breeding is essential but it is a long drawn process, whereas PGPR inoculation to alleviate drought stresses in plants opens a new chapter in the application of microorganisms in dry land agriculture. Taking the current leads available, concerted future research is needed in terms of identification of the right kind of microbes and addressing the issue of delivery systems and field evaluation of potential organisms

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